

## Pheromone-Induced Movement of Nymphs of the Predator, *Podisus maculiventris* (Heteroptera: Pentatomidae)

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Males of the generalist predator, *Podisus maculiventris* (Say) (Heteroptera: Pentatomidae) (known as the spined soldier bug), attract mates with a pheromone, but the immature stages of the predator also appeared to be attracted. Therefore, attraction of nymphs of *P. maculiventris* to pheromone was studied in a wind tunnel and in field plots. The behavior of individual nymphs toward pheromone with and without Colorado potato beetles, *Leptinotarsa decemlineata* (Say) (Chrysomelidae), and/or potato plants in the airstream was studied in a wind tunnel. Field experiments were performed in plots planted with green beans, *Phaseolus vulgaris* L. that were allowed to become naturally infested with Mexican bean beetles, *Epilachna varivestis* (Moulsant) (Coccinellidae). Spined soldier bug nymphs were released in the middle row of plots planted for 3 weeks, and three commercial pheromone dispensers were placed outside the thirteenth row of a plot. *Podisus maculiventris* nymphs were significantly attracted to synthetic pheromone both in the laboratory and in the field. Results of wind tunnel experiments indicated that combining the pheromone with the phytophage significantly increased the positive responses of nymphs compared to the pheromone alone; however, inclusion of damaged or undamaged potato plants with pheromone did not enhance the positive responses to the odor source. Spined soldier bugs released in field plots remained relatively sedentary for the first day after release, but by the end of the 1-week sampling period nymphs had significantly moved into rows nearer the pheromone dispensers. The ability to manipulate immature spined soldier bugs significantly expands the potential for using this generalist predator in integrated pest management programs. © 1997 Academic Press

**KEY WORDS:** Spined soldier bug; Colorado potato beetle; Mexican bean beetle; Hemiptera; pheromone; augmentation; biological control.

### INTRODUCTION

The spined soldier bug, *Podisus maculiventris* (Say) (Heteroptera: Pentatomidae), is a predator of a wide variety of defoliating insects in North America (McPherson, 1982), including pests such as the Mexican bean beetle, *Epilachna varivestis* (Moulsant) (Coccinellidae) (O'Neil, 1988), and the Colorado potato beetle, *Leptinotarsa decemlineata* (Say) (Chrysomelidae) (Ruberson *et al.*, 1987). Augmentation of spined soldier bugs has shown promise for suppression of Colorado potato beetle infestations, as has augmentation of the twospotted stink bug, *Perillus bioculatus* (F.) (Boiteau, 1988; Biever and Chauvin, 1992; Hough-Goldstein and Whalen, 1993). However, the spined soldier bug is more fecund than *P. bioculatus* and can eat at least as many Colorado potato beetle eggs and larvae as the twospotted stink bug (Hough-Goldstein and McPherson, 1996).

Spined soldier bug predation efficiency is principally affected by its ability to find prey and by the number and type of prey present in the environment (Wiedemann and O'Neil, 1992; Legaspi and O'Neil, 1993). Encountering prey is also related to plant growth since spined soldier bugs search relatively less area as leaf area increases. Suboptimal searching efficiency by *P. maculiventris* nymphs results in lower weight, slower development, and fewer nymphs reaching adulthood (Legaspi and O'Neil, 1994). Moreover, the adults that develop under these conditions are weaker and less fecund (Evans, 1982; Wiedemann and O'Neil, 1990). Nevertheless, *P. maculiventris* individuals can survive extended periods of prey scarcity by feeding on plants (Ruberson *et al.*, 1987; Valicente and O'Neil, 1995). One way to maximize the effectiveness of *P. maculiventris* as a biological control agent would be to enhance its searching efficiency, particularly that of the nymphs.

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Adult males of *P. maculiventris* produce an attractant pheromone (Aldrich *et al.*, 1984; Aldrich, 1995), and a Soldier Bug Attractor is commercially available (Anonymous, 1992). The objective of the present study was to determine in the laboratory the extent to which nymphs are attracted to the pheromone and to determine if the synthetic pheromone could be used to increase movement of *P. maculiventris* nymphs from release points in the field.

## MATERIAL AND METHODS

### Wind Tunnel Experiments

**Insects.** A colony of *P. maculiventris* started from specimens collected at the Beltsville Agricultural Research Center in the summer of 1993 was maintained in Italy for wind tunnel experiments, and additional wild adults from Beltsville were added to the Italian colony in 1994. The bugs were reared on mealworm larvae and pupae (*Tenebrio molitor* L. [Coleoptera: Tenebrionidae]), green beans (*Phaseolus vulgaris* L.), and water at  $25 \pm 2^\circ\text{C}$ , 70% relative humidity, and a 16:8 h light:dark photoperiod. Colorado potato beetles were collected in the field near Perugia in Coliflorito, Italy, and maintained on potato plants in a greenhouse until use. Wind tunnel experiments were completed in the winter of 1994–1995.

**Wind tunnel.** A  $2 \times 0.5 \times 0.5$ -m rectangular wind tunnel was constructed of plexiglass held in place by an aluminum frame, and the tunnel was marked exteriorly into six equal zones for scoring the movement of bugs during bioassays. Charcoal-filtered air was blown into the tunnel from one end by a fan through a baffle array, and the exhaust went from the other end to the exterior of the building. The flow pattern was checked using titanium tetrachloride vapors, and the intake baffles were adjusted to produce a laminar flow. Air speed was measured using an anemometer (Model TA 6000, Airflow Developments, Ltd., High Wycombe, England) and adjusted to 0.4 m/s. Light was provided by six high-frequency lamps (Philips TLD 50W) along the top of the tunnel which yielded 1700–1800 lux of illumination. Temperature and relative humidity in the room containing the wind tunnel were maintained at  $25 \pm 2^\circ\text{C}$  and 70%, respectively. A continuous canopy was created in the tunnel by placing 36 pots of sand inside, half with artificial plastic plants and half with artificial cloth plants, with the artificial foliage overlapping so as to provide a substrate on which nymphs could walk.

**Bioassay.** Before each test, except for control tests, scent source material(s) was placed in the upwind compartment of the wind tunnel designated "source." The various treatments tested are listed and described in Table 1A. Ten Colorado potato beetles (third- and fourth-stage larvae and adults) were fed potato plants

TABLE 1

Treatments Tested in Wind Tunnel Bioassays (A) and Behavioral Events Recorded for *Podisus maculiventris* Nymphs Responding to Treatments (B)

A		
Scent source	Code	Description
Control	CTRL	No scent material in source area
Potato plant	P	Two 30-cm-tall, uninjured plants
Phytophage	CPB	Ten beetle larvae in mesh bag
Pheromone	PH	Five microliters pheromone/cotton wick
Plant-phytophage	P + CPB	Two plants with beetle larvae
Phytophage-pheromone	CPB + PH	Beetle larvae in bag and pheromone
Plant-phytophage-pheromone	P + CPB + PH	Infested plants and pheromone
B		
Behavioral event	Description	
Inactivity	Insect immobile with antennae lowered	
AlertTposture	Antennae raised and vibrated; body rotated laterally	
Grooming	Cleaning antennae with its tibial combs	
SlowlyTwalking	Walking, occasionally touching substrate with antennae and/or rostrum	
RapidlyTwalking	As above but quicker and more directed	
ProbingTplant	Extension of rostrum in feeding posture	

for 2–3 days prior to use in the complex "plant-phytophage" (P + CPB) bioassay. To initiate a test, a fourth- or fifth-instar *P. maculiventris* nymph was released in the wind tunnel 130 cm from the upwind end. Nymphs used in bioassays were fed Colorado potato beetle larvae 1–2 days prior to testing and then held with only moist cotton until tested. A test was considered completed when the nymph reached the source area or after 30 min. The behaviors of each nymph tested were recorded on a personal computer using the "Observer 3.0" program (Noldus Technologies, Wageningen, The Netherlands). The behavioral events registered are listed in Table 1B. Ten replicates were run for each treatment.

**Statistical analysis.** Behavioral data, expressed as percentages of time spent exhibiting each type of behavior per zone, were normalized by an arc sine square root transformation. Means of different treatments were compared with the Waller–Duncan test ( $P < 0.05$ ). Untransformed means, expressed as percentages, are reported.

### Field Experiment

**Insects.** Adults of *P. maculiventris* were collected in the field at the Beltsville Agricultural Research Center (BARC) using traps baited every 2–3 days with a blend

of (*E*)-2-hexenal,  $\alpha$ -terpineol, and benzyl alcohol as previously described (Aldrich *et al.*, 1984; Aldrich, 1997). The traps were positioned every 20 m or so at ca. 2 m above the ground in deciduous trees (primarily oak) bordering agricultural fields and powerlines. Adult spined soldier bugs were collected from traps at least four times a week from mid-March to mid-May 1995. The wild adults were kept in growth chambers for several weeks at ca. 10°C to delay production of *P. maculiventris* nymphs until bean beetles appeared in the field. Mass production of late-stage spined soldier bug nymphs synchronously with bean beetle infestations of plots was accomplished by periodically moving groups of wild *P. maculiventris* adults to a growth chamber operated at  $26 \pm 2^\circ\text{C}$ ,  $60 \pm 5\%$  relative humidity, and a 16:8 h light:dark photoperiod. Groups of about 10 adult males and females were confined in half-pint cartons provided with a water bottle, a fresh green bean, and mealworm pupae every 2–3 days, along with a piece of cheesecloth as an oviposition substrate. Cheesecloth pieces were replaced in oviposition cartons at least twice a week, and cheesecloth pieces with *P. maculiventris* eggs were transferred to new cartons to rear fourth- and fifth-instar nymphs for release in field plots.

**Field plot bioassay.** Green beans (*P. vulgaris*) were planted in plots every 2 weeks at BARC–West beginning in late June 1995. Each plot (9.7  $\times$  6.3 m) consisted of 13 rows (ca. 40 plants/row; 75 cm between rows). Field tests were conducted from July 10 to August 15, 1995. A test started when the plants in a plot were 3 weeks old (phase: G3), by which time they were naturally infested with Mexican bean beetles. To start a test, three Soldier Bug Attractors (Sterling International, Inc., Liberty Lake, WA) were placed in the ground along the outside border of the thirteenth row of the plot, and then third- and fourth-instar *P. maculiventris* nymphs were released throughout the seventh row of the plot (seven replicates; 150 to 450

nymphs being released per plot, average/plot = 261 nymphs). Releases were made in late afternoon in an effort to minimize mortality. Counts of spined soldier bug nymphs and of Mexican bean beetles were made 1, 4, and 7 days after release by inspecting four randomly chosen 30-cm portions of each row.

**Statistical analysis.** The mean number of insects was summed across the rows for each sample, direction (treated = Rows 8–13; untreated = Rows 1–6), and plot combination. These variables were then analyzed as three factor general linear mixed models using PROC MIXED (SAS Institute, 1996). Direction and sample were the fixed effects, and plot was the random factor. Variance grouping was done to correct for variance heterogeneity in the variables. The least-squares means and standard errors of the means were calculated, and pair-wise comparisons of the means were performed.

## RESULTS

### Wind Tunnel Experiments

Bioassays were analyzed according to the average time spent in each zone of the wind tunnel, and the average duration of each type of behavior (Table 1). The time spent by nymphs in the upwind zone (nearest the scent source) provided the clearest representation of responses to the various treatments (Table 2). *Podisus maculiventris* nymphs spent practically no time in the upwind zone when there was no scent source (CTRL). Potato plants alone (P) or beetles alone (CPB) elicited higher responses, but there was no enhancement of the response by the combined P + CPB treatment, and none of these treatments were significantly different from each other. Pheromone alone (PH) caused nymphs to spend significantly more time in the upwind zone relative to CTRL and P + CPB treatments; however, the response to the PH treatment did not significantly exceed responses to P and CPB treatments. The combi-

TABLE 2

Behavior of *P. maculiventris* Fourth- and Fifth-Stage Nymphs in a Wind Tunnel in Response to Plant, Pheromone, and Phytophage Treatments

Treatments	% Time in upwind zone ( $\pm$ SEM) <sup>a</sup>	% Time spent exhibiting each behavior ( $\pm$ SEM)					
		Inactivity	Alert posture	Grooming	Slowly walking	Rapidly walking	Probing plant
Control	0.0 $\pm$ 0 d	54.2 $\pm$ 6.8 ab	5.5 $\pm$ 1.60 de	2.4 $\pm$ 0.5 a	33.4 $\pm$ 5.0 ab	3.6 $\pm$ 2.4 b	0.9 $\pm$ 0.4 b
Potato plant	5.1 $\pm$ 3.2 cd	45.6 $\pm$ 10.9 abc	11.3 $\pm$ 4.5 cde	4.6 $\pm$ 2.4 a	33.6 $\pm$ 6.0 ab	3.9 $\pm$ 2.6 b	1.0 $\pm$ 0.7 b
Phytophage	6.9 $\pm$ 4.3 bcd	27.9 $\pm$ 8.1 cd	19.9 $\pm$ 4.9 b	3.7 $\pm$ 0.9 a	34.5 $\pm$ 6.0 ab	9.5 $\pm$ 3.7 b	4.5 $\pm$ 2.7 b
Pheromone	20.5 $\pm$ 6.4 bc	38.5 $\pm$ 6.9 bc	12.5 $\pm$ 2.1 bcd	4.0 $\pm$ 0.7 a	36.5 $\pm$ 3.7 ab	5.8 $\pm$ 1.6 b	2.7 $\pm$ 4.5 b
Plant-phytophage	1.1 $\pm$ 1.1 d	64.4 $\pm$ 10.5 a	2.9 $\pm$ 1.4 e	6.5 $\pm$ 2.7 a	24.9 $\pm$ 7.6 b	1.3 $\pm$ 1.2 b	0.0 $\pm$ 0.0 b
Phytophage-pheromone	37.4 $\pm$ 11.1 a	9.1 $\pm$ 3.7 d	34.8 $\pm$ 5.0 a	2.9 $\pm$ 0.5 a	31.3 $\pm$ 5.9 ab	21.7 $\pm$ 7.3 a	0.2 $\pm$ 0.2 b
Plant-phytophage-pheromone	21.6 $\pm$ 7.3 ab	12.7 $\pm$ 6.9 d	15.1 $\pm$ 3.0 bc	5.6 $\pm$ 1.9 a	48.9 $\pm$ 7.2 a	5.0 $\pm$ 1.9 b	12.8 $\pm$ 6.1 a

<sup>a</sup> Values followed by different letters are significantly different ( $P \leq 0.05$ ) according to the Waller test.

TABLE 3

Interaction between Days after Release and Mean Number of *P. maculiventris* Nymphs Sampled in Each Treatment in Field Trials

Treatment	Days after release <sup>a</sup>		
	1	4	7
Control	1.71 ± 0.54 a	1.00 ± 0.54 a	1.00 ± 0.54 a
Pheromone	3.29 ± 1.21 a	6.29 ± 1.21 b	3.00 ± 0.54 b

<sup>a</sup> Means followed by the same letter are not significantly different ( $P \leq 0.05$ ).

nation of pheromone with beetles (PH + CPB) caused *P. maculiventris* to spend over 35% of their time in the upwind zone. This treatment effect was significantly greater than that of all other treatments except the plant-phytophage-pheromone treatment (P + CPB + PH).

Significant treatment differences were also found in the duration of inactivity, alerted posture, rapid walking, and plant probing (Table 2). The percentages of time spent inactive were lowest for the CPB + PH and P + CPB + PH treatments, and these treatment effects were significantly different from those of all others except for the CPB treatment. The times spent by nymphs in an alerted posture and rapidly walking in response to the CPB + PH treatment were significantly greater than those for all other treatments. Finally, the plant-phytophage-pheromone treatment (P + CPB + PH) provoked attempts to feed on the plastic plants composing the artificial canopy which were significantly longer than feeding attempts in response to all other treatments. In addition, nymphs were sometimes observed attempting to feed directly on the cotton wick impregnated with synthetic pheromone.

#### Field Experiment

It was estimated that 25–50% of the spined soldier bug nymphs died shortly after release, apparently from the stress of handling and from adverse environmental conditions such as hot summer temperatures and rain. Despite the relatively low numbers of nymphs recorded in the samplings, there were significantly more nymphs found in Rows 8–13 (nearest the pheromone dispensers) than in Rows 1–6 on Days 4 and 7 after release (Table 3). Figure 1 shows the mean movement pattern of *P. maculiventris* nymphs in field plots at 1 day (A), 4 days (B), and 7 days (C) after release on the middle row of plots (Day 0).

Table 4 shows a breakdown of the mean number of nymphs observed for each treatment as a function of nymphal instar. While the distribution of the combined nymphal instars was highly significantly skewed toward the pheromone sections of plots ( $P \leq 0.001$ ), only

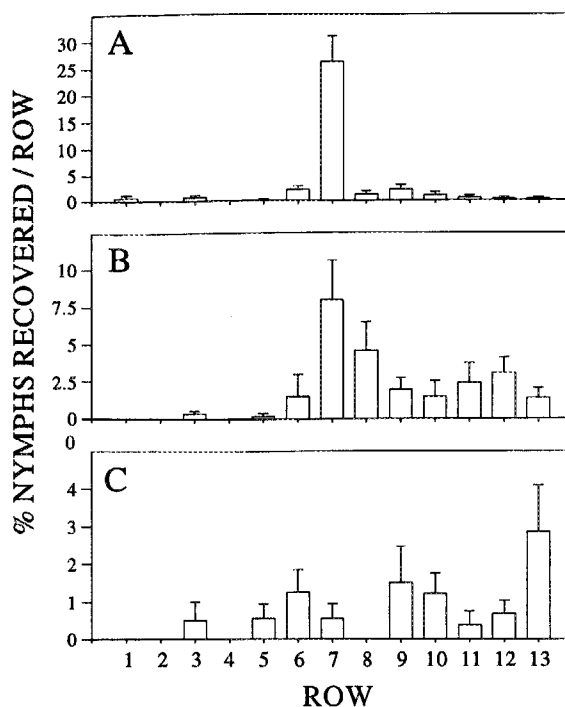


FIG. 1. Mean percentage recovery per row ( $\pm$ SEM) of *Podisus maculiventris* nymphs 1 day (A), 4 days (B), and 7 days (C) after release on Row 7 in plots with pheromone dispensers placed on the outside of Row 13 (details in text).

the difference for the fourth-instar nymphs was significant ( $P \leq 0.006$ ).

The distributions of Mexican bean beetle eggs, larvae, and adults were not significantly different across rows for any of the sampling periods. *P* values for total numbers of bean beetle egg masses, larvae, and adults at 1 day, 4 days, and 7 days were  $P = 0.1360$ ,  $P = 0.5070$ , and  $P = 0.7173$ , respectively. Figure 2 shows the mean number of bean beetle larvae per row sampling at 1 day (A), 4 days (B), and 7 days (C).

#### DISCUSSION

*P. maculiventris* nymphs were significantly attracted toward synthetic pheromone both in the laboratory and

TABLE 4

Mean Number of *P. maculiventris* Nymphs Observed in Each Treatment in Field Trials

Treatment	Nymphal instar <sup>a</sup>			Combined instars
	Third	Fourth	Fifth	
Control	0.48 ± 0.19 a	0.48 ± 0.27 a	0.29 ± 0.10 a	1.24 ± 0.35 a
Pheromone	1.52 ± 0.46 a	2.10 ± 0.33 b	0.57 ± 0.19 a	4.19 ± 0.58 b

<sup>a</sup> Means followed by the same letter are not significantly different ( $P \leq 0.05$ ).

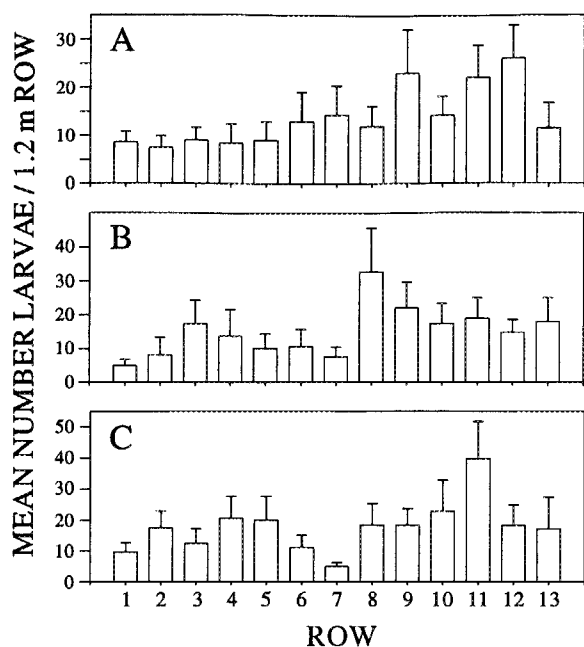


FIG. 2. Mean number of *Epilachna varivestis* larvae per row sampling ( $\pm$  SEM) at 1 day (A), 4 days (B), and 7 days (C).

in the field. Results of wind tunnel experiments indicated that combining the pheromone with larvae of the Colorado potato beetle significantly increased the positive responses of nymphs compared to those of the pheromone alone. However, inclusion of potato plants with pheromone did not enhance the positive responses to the stimulus source. Spined soldier bug nymphs released in a field row-crop environment remained relatively sedentary for the first day after release, which is consistent with earlier results (Waddill and Shepard, 1975), and mortality appeared to be high during this time period. Eventually, however, significantly more surviving nymphs moved into rows nearer the pheromone dispensers than into rows further from the dispensers.

Shetty and Hough-Goldstein (1996) found that fifth-instar spined soldier bug nymphs from a 2-year-old laboratory colony did not significantly respond to pheromone in a wind tunnel. However, these authors also showed that adult spined soldier bugs which were three generations or less removed from wild-caught *P. maculiventris* adults responded significantly more to pheromone in the wind tunnel than did adult bugs from the 2-year-old laboratory colony. The fourth- and fifth-instar *P. maculiventris* nymphs used in our wind tunnel experiments were not highly inbred, but data for these instars were grouped for analysis. The distributions of *P. maculiventris* nymphs released in our field experiments were analyzed by instar and, interestingly, only fourth-instar nymphs were significantly more abundant in rows nearest the pheromone dispensers.

Our study is apparently the first experimental at-

tempt to attract immature predators in the field with a synthetic pheromone. In these field experiments, pheromone dispensers were always positioned on the southwest end of plots so that pheromone tended to blow into plots by the predominantly westerly winds. The distribution of Mexican bean beetles did not differ significantly across the 13-row plots, suggesting that movement of spined soldier bug nymphs was not a response to prey-associated volatiles. Nevertheless, field experiments need to be repeated to determine the extent to which *P. maculiventris* nymphs may respond to other cues such as wind or volatiles from prey-infested plants. Also, further research is needed to determine if the nymphal instars of the spined soldier bug actually do differ in their response to pheromone.

Why should spined soldier bug nymphs be attracted to a pheromone that evolved in males as a mechanism to attract potential mates? One possibility is that the presence of pheromone is associated with available prey (Aldrich, 1995). Similarly, Leal *et al.* (1995) postulated that attraction of nymphs of the bean bug, *Riptortus clavatus* (Thunberg) (Alydidae), to pheromone from conspecific adult males is an adaptive response to locate food plants. For *P. maculiventris*, this explanation for the attraction of nymphs to pheromone occurred to us when we observed that nymphs in wind tunnel experiments salivate and apparently imbibe the pheromone upon arriving at the source. Laboratory bioassays with *Podisus nigrispinus* (Dallas) and a related predator, *Supputius cincticeps* (Stål), showed that treating artificial diet with an extract of adult male pheromone glands significantly reduced the time required to locate the diet and improved feeding on the diet (Torres *et al.*, 1997). These data, along with the demonstration by Pfannenstiel *et al.* (1995) that spined soldier bugs are attracted to the vibrations produced by feeding caterpillars, indicate that the search for prey by *P. maculiventris* is less random than previously thought (Heimpel and Hough-Goldstein, 1994; Wiedenmann and O'Neil, 1991).

Because generalist predators such as the spined soldier bug maintain large, widespread populations, it may be practical to harvest wild adults in pheromone-baited traps to mass-produce young predators for augmentative biological control (Aldrich, 1997). The discoveries that the immature stages of *P. maculiventris* are apparently attracted to synthetic pheromone, and are stimulated to search for and to feed on prey when exposed to pheromone, open new avenues for manipulation of this beneficial insect. For example, synthetic pheromone could be useful in moving young predators from points of release or into successive plantings of vegetables, and combining pheromone with artificial diet may promote diet location and acceptance by the bugs.

In recent years some researchers have questioned whether the importation of exotic biocontrol agents is

worth the risk of adverse effects to innocuous and beneficial endemic species (Simberloff and Stiling, 1996, and references therein). Currently, there seems to be an increased awareness of the benefits of practicing agriculture in a way that promotes the activities of native predators (Kareiva, 1996; Settle *et al.*, 1996). In vegetable production, significant advances have been made toward sustainability with reduced inputs of herbicides and synthetic fertilizer (e.g., Abdul-Baki *et al.*, 1996). To complement this sustainable vegetable production system, biological control of pests needs to be incorporated in the management scheme. Conservation and augmentation of *P. maculiventris* can contribute to biological control of a variety of vegetable pests. The judicious utilization of the synthetic pheromone of this native predator should increase the chances of its success as a biological control agent.

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